

THE EVOLUTIONARY SIGNIFICANCE OF
REDUNDANCY AND VARIABILITY IN
PHENOTYPIC-INDUCTION MECHANISMS OF
PIERID BUTTERFLIES (LEPIDOPTERA)*

BY ARTHUR M. SHAPIRO
Department of Zoology
University of California
Davis, California 95616, U.S.A.

One of the major discoveries in the study of seasonal polyphenism in butterflies was the role of larval photoperiodic exposure (Danilevskii, 1948). Following this discovery, experiments on two Pierid species — *Colias eurytheme* Bdv. (Watt, 1969; Hoffman, 1974) and *Pieris protodice* Bdv. & LeC. (Shapiro, 1968) — appeared to establish that temperature played no role in the seasonal polyphenisms of that family. This was clearly not the case in at least one Nymphalid, *Araschnia levana* (L.): Süffert (1924) had shown a temperature effect, and later work by Danilevskii (1948), Müller (1955, 1956, 1960), Reinhardt (1969, 1971), and Müller and Reinhardt (1969) showed that photoperiod and temperature interact in a characteristic way. Long-day larvae or young pupae, normally destined to produce the summer form *prorsa*, if experimentally cooled will produce either the winter form *levana* or an intermediate form (*porima*). Short-day larvae give rise to diapause pupae which always give *levana*, regardless of temperature. Thus photoperiod, acting on 4th- and 5th-instar larvae, can irreversibly determine the vernal phenotype, but not the estival one, which can be overridden by temperature acting on the young pupa.

Shapiro (1977) established that pupal diapause and adult phenotype, normally tightly coupled in the *Pieris napi* (L.) group of Pieridae, could be decoupled in *P. n. venosa* Scudder. In *napi* generally, diapausing pupae give rise to vernal phenotypes and non-diapausing ones to estival phenotypes. Populations consist of a mixture of obligate diapausers, apparently determined genetically, and facultative ones responsive to daylength. In some but not all populations, inducing photoperiods can be overridden by high

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developmental temperatures, but low temperatures cannot induce diapause in long-day animals. (This system was first demonstrated for *P. rapae* (L.) by Barker, Mayer, & Cohen (1963).) When non-diapause, long-day pupae of *P. n. venosa* are chilled, they produce vernal phenotypes; thus diapause is not necessary to produce them. However, it is not known whether all diapause individuals are irreversibly determined phenotypically, because they have a mandatory chilling requirement and break diapause in mid-winter, thus assuring that every individual will receive some post-diapause chilling. The entire system is summarized in Fig. 1.

Although the necessary experiments to clarify this point have not been completed with *P. n. venosa*, they have been in the literature for 50 years in a very important paper which has been universally overlooked by English-speaking workers (Lorković, 1929). Lorković worked with *P. rapae* and, to a lesser extent, *Pontia daplidice* (L.). It is worth quoting at some length from a translation of the summary ("homodynamic" pupae are non-diapausers; "heterodynamic" are diapausers):

"Not only the homodynamic but also the heterodynamic pupae of *P. rapae* are strongly influenceable in respect to the butterfly's markings. If the homodynamic pupae are put in heat (25–30° C) during the sensitive period (which at 25° sets in about 12 hours after pupation), they produce strongly black-spotted butterflies, while cold (5° C) brings about a disappearance of these spots as well as a densely dark powdering of the hindwing underside. Naturally there are formed at corresponding temperatures also all intermediates between the two extremes. The heterodynamic pupae produce as a whole intermediate forms . . . but, contrary to the results of Süffert (on *A. levana* — A.M.S.), the heat form can also be produced by a high temperature of 32° C; but the black marking of the forewing always approaches the heat form more than the hindwing underside, which can never attain the extreme grade of the heat form. At lower temperatures the spotless form is occasioned. The influencing of the heterodynamic pupae by temperature is successful only during the last section of development; pupae which for 3 months were kept at lower temperatures (–5° to +10°) produced heat forms after 6–8 days of exposure to higher temperature (32°).

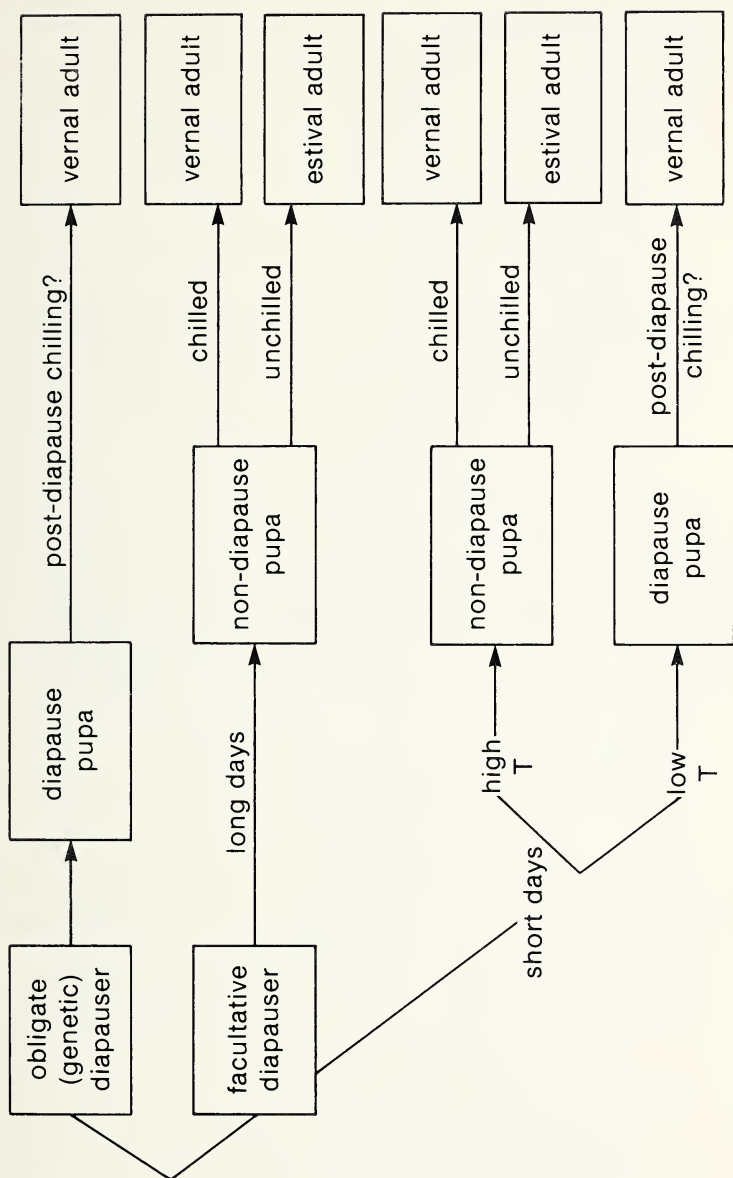


Fig. 1. Schematic representation of developmental and phenotypic options available to *Pieris napi*. Not all options found in all populations, but all except those queried have been demonstrated in the laboratory.

(Lorković used pupal weight to estimate time of breaking of diapause. — A.M.S.) It must therefore be taken that the “heterodynamic sensitive period” sets in only after the completed latency. (Compare *Papilio zelicaon* Lucas, Shapiro, 1976. — A.M.S.) There are species in which the duration of the pupal dormancy shows great lack of uniformity, varying from 1–8 years, without the difference being reflected at all in the markings of the butterflies . . .”

Indications of the same phenomena are apparent in temperature-manipulation experiments with the aforementioned *P. protodice* and *C. eurytheme*, which had been thought to employ photoperiodic cues alone. In both species vernal phenotype is irreversibly determined by short days (actually long nights), regardless of temperature and with no linkage to diapause (there are no obligate diapausers in *P. protodice*, and *C. eurytheme* has no diapause at all). However, as in both *A. levana* and *P. n. venosa*, long-day animals can be induced to develop the full vernal phenotype by pupal chilling. Examples are shown in Fig. 2. That these responses have been missed in the past is not surprising; they are difficult to work with. In a given group of sibs a few individuals will respond strongly to a given treatment, while others respond slightly or not at all. It is difficult to keep track of precise pupation times for large numbers of individuals and to obtain statistically meaningful numbers of even-aged pupae for treatment, and the precise characterization of the responses will take several years, just as it did for the Nymphalid *Nymphalis urticae* (L.) (history reviewed in Shapiro, 1976). However, it is already clear that there is considerable intrapopulational variability in the timing of the “sensitive period,” that it is quite short (there is no statistical difference in the distribution of phenotypes in batches of *P. protodice* chilled at the same age and held for 1, 2, 3, or 4 weeks), and that the mean responses among geographic conspecific populations differ.

Precisely the same phenomena emerge in previous studies of phenotypic plasticity which is not involved in regular seasonal polyphenism: *Aricia* spp. (Hoegh-Guldberg, 1974a, b; Jarvis, 1974) (Lycaenidae); various moths (Kettlewell, 1963); and especially the “elymi” series of aberrations in *Vanessa* spp., and similar aberrations in *Nymphalis* spp. (all Nymphalidae; see Shapiro, 1976). These temperature-induced variations are “morphoses” (Schmalhausen,

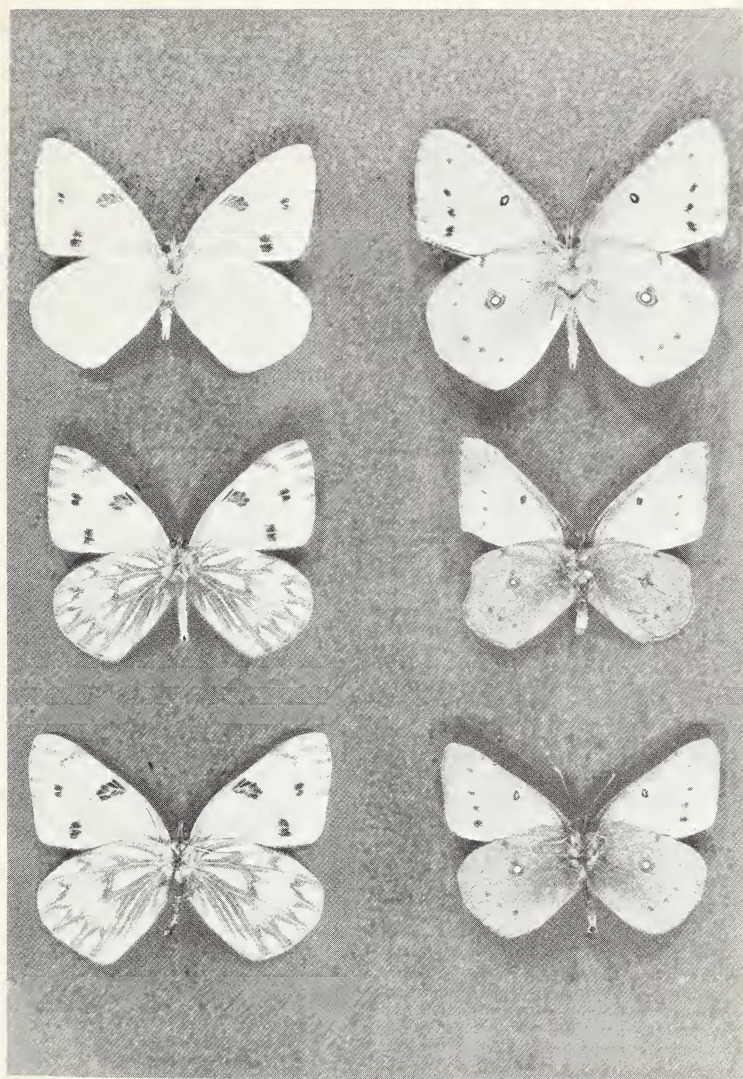


Fig. 2. Examples of redundant mechanisms in phenotypic induction. Ventral surfaces of males of *Pieris protodice* (left) and *Colias eurytheme* (right). Top: estival phenotypes, 24 L:O D, 25° C, pupa unchilled. Center: vernal, same conditions, young pupa chilled. Bottom: vernal, 10L: 14D, 25° C, pupa unchilled.

1949), nonadaptive developmental reactions. But the reactions of Pierids are the same as those regularly produced by photoperiod, and are presumably *adaptive*.

Probably most or all individuals of *P. protodice* and *C. eurytheme* can be switched from an estival to a vernal phenotype by some degree of chilling at some time in the first 24 hours after pupation. If this is true, then temperature can reinforce photoperiod in producing seasonally appropriate adult phenotypes in multivoltine species. For diapaused individuals of *P. protodice* and the closely related *P. occidentalis* Reak., the irreversibly determined vernal phenotype may be reinforced by post-diapause chilling, producing the characteristically greater phenotypic expression than is seen in lab-reared animals. The same is perhaps true for the (non-diapausing) late winter pupae of *C. eurytheme*. The period of post-diapause or late-winter chilling is so prolonged in the wild that virtually all overwintered animals will be affected. This process will tend to smooth over, or conceal, not only the aforementioned genetic variance in "sensitive period" but that which characteristically occurs for chilling requirement (strength of diapause), as well. Yet all of this variance is potentially adaptive in fluctuating environments, particularly when the suitability of spring weather for butterflies is highly uncertain, and we should expect selection to match norms of reaction to environmental uncertainty in populations with sufficient genetic integrity. Does it?

Hoffman (1978) reports that Rocky Mountain *Colias philodice eriphyle* Edw. differs from both *C. eurytheme* and *C. p. philodice* Godart in having adult phenotype decoupled from photoperiodic control (though it may be temperature-sensitive). He attributes this to high environmental uncertainty which renders photoperiod a poor seasonal predictor. Similar predictions about developmental phenology were made by Bradshaw (1973) and Istock (1978). Similarly, Shapiro (1973) found phenotype less reliably cued by photoperiod in the montane *Pieris occidentalis* than in *P. protodice*, a lowland species. Crosses of *C. p. philodice* × *C. p. eriphyle* would be informative as to how simple or complex genetic control of photoperiodic coupling can be. Right now everything which is known points to a definite evolutionary sequence in the history of insect polyphenism: a pre-existing phenotypic response to temperature which happens to be adaptive in some environments but not others is subject to selection for modifiers which affect threshold of

expression and ultimately couple it to a reliable seasonal predictor, normally a pre-existing photoperiodic control of diapause.

This postulated evolutionary sequence can be further rationalized by noting that the pattern of interaction among genetics, photoperiod, and temperature is completely in accord with Darwinian predictions. For multivoltine species, which in Pieridae are weedy colonizers, photoperiodic determination of diapause can be overridden by high temperature in some individuals, allowing them to gamble on an extra generation in an unusually warm autumn. But photoperiodic determination of vernal phenotype is absolute; this makes sense insofar as autumn is colder than summer and any direct-developing butterflies will be aided in their feeding and reproductive activities by the thermoregulatory properties of the vernal phenotype. Estival phenotypes are not irreversibly determined by summer photoperiods. Cold can act on the young pupa just a few days before hatch to produce more or less of the vernal phenotype, giving rise to darker animals on short notice in unseasonably cold conditions. Hoffmann's Rocky Mountain *C. p. eriphyle* and Shapiro's coastal *P. n. venosa* are commonly exposed to unseasonable cold and switch readily without regard to photoperiod. But lowland *C. eurytheme* and *P. protodice*, which rarely face such conditions, are arcane enough in their "sensitive period" characteristics that they were missed altogether in laboratory experiments for years.

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